PNAS RESEARCH ARTICLE | ECOLOGY OPEN ACCESS

Sub-ice thermal gradients strongly influence winter depth use of an iconic cold-water fish

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Edited by Mary E. Power, University of California Berkeley, Berkeley, CA; received January 12, 2026; accepted September 11, 2026

In a thermally stratified lake, freshwater fish select habitats that align with their thermal preferences. While most studies of dimictic lakes have focused on habitat selection during summer stratification, less attention has been given to winter when inverse thermal stratification occurs with water temperatures between 0 to 4 °C. Our results show that winter thermal stratifications vary considerably among lakes. Much of the variation in winter depth use by the cold-water predator, Lake Trout (*Salvelinus namaycush*), can be explained by the depth of the 2 °C isotherm. Selection ratios further support preferential use of this thermal boundary after accounting for habitat availability. Larger, shallower, and windier lakes tend to exhibit colder mean temperatures near 0 °C and deeper isotherms, typically within the 1 to 2 °C range. In contrast, deeper or more sheltered lakes maintained warmer temperatures close to 4 °C and a shallower 2 °C isotherm. Using multiyear acoustic telemetry of Lake Trout from 11 different lakes, we found that in warmer lakes with depth-averaged temperatures above 2 °C, Lake Trout used thermal habitat averaging 2.6 ± 0.6 °C, which occurred in relatively shallow depths (0.1 to 11.3 m). In contrast, in the one large, shallow lake studied, where maximum water temperatures were below 2 °C, Lake Trout occupied the deepest waters during winter (16.8 to 26.4 m) and experienced average temperatures of 1.5 ± 0.4 °C. Applying our model to 877,927 Canadian and Alaskan lakes predicted a roughly even split between warm and cold winter conditions; however, 73% of the 66,500 known Lake Trout lakes exhibited warmer winter conditions, where Lake Trout would occupy the upper water column during winter.

inverse thermal stratification | thermal biology | cold-water fish | ice-covered lake | habitat selection

Significance

Understanding fish habitat selection during the winter ice-covered period in northern lakes is critical for predicting species distributions under climate warming. Using 32 y of acoustic telemetry from 11 North American lakes, this work shows how Lake Trout, a cold-water top predator, adjusts winter habitat use in response to differences in thermal structure across lakes with different morphometry and wind exposure. Lake Trout preferentially selected depths near the 2 °C isotherm after accounting for depth-specific habitat availability, with this selected depth occurring deeper in large, wind-exposed lakes, and shallower in smaller, sheltered lakes. Integrating multilake telemetry with predictive modeling offers a scalable framework for assessing winter thermal habitat availability and forecasting ecological responses of Lake Trout to changing ice and thermal regimes.

Fish are ectotherms and their metabolism is closely related to water temperature (1, 2). In freshwater lakes with vertical thermal gradients, fish actively select habitats that align with their thermal preferences (3). The most common class of lakes in North America are dimictic lakes, which are thermally stratified in summer, mix vertically in spring and fall, and can have an inverse thermal stratification under the ice during winter. In summer, dimictic lakes usually have three distinct layers: a surface warm epilimnion, which can be as warm as 20 to 24 °C, a metalimnion at mid-depths where vertical temperature gradients exceed 1 °C m^{-1}, and a deep hypolimnion where temperatures are usually close to 4 °C (the temperature of maximum density of water). Broadly speaking, fish can be classified into three thermal guilds based on their preferences: cold-water, cool-water, and warm-water (4), with optimal temperatures <17.5 °C, 17.5 to 25 °C and >25 °C, respectively. The thermal niche of most fishes typically falls within ±2 °C of their preferred temperatures (4, 5). Thus, in summer, cold-water fish are typically found in the hypolimnion below the thermocline, cool-water fish within the metalimnion, and warm-water fish are found in the epilimnion. In winter, vertical temperature gradients persist but are much weaker and far less studied than those in summer (6), despite widespread ice cover across northern lakes (7–9). Inverse thermal stratification develops in ice-covered lakes because freshwater has its maximum density near 4 °C, causing colder, lighter water to remain beneath the ice while warmer water occupies deeper layers (10). Although the winter thermal range (0 to 4 °C) is narrower than in summer, it remains large compared to the narrow ±2 °C thermal niche of stenothermal fishes identified by Magnuson et al. (4). With the advent of year-round monitoring of fish space use by biotelemetry combined with high-resolution temperature profiles, it is now possible to explore how fish occupancy relates to winter thermal habitat (5, 7).

The exact form of inverse stratification present during winter can vary dramatically among lakes of different geometry, as well as between years in individual lakes (11). Once

The authors declare no competing interest.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2600502123/-/DCSupplemental.

Published November 9, 2026.

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surface ice forms and effectively shields the lake from further wind-driven mixing, the heat fluxes to the lake are much smaller and subsequent changes in thermal stratification proceed at a markedly reduced rate (12). Consequently, the wind-driven mixing that occurs just before ice-on is key to determining the temperature profile of the water column during winter. In lakes with large surface area-to-depth ratios, strong winds can keep the water column well mixed as it cools down, so that when ice forms, the entire water column is nearer 0 °C. In contrast, many deeper lakes, especially those that are sheltered from strong winds by forests, may experience limited wind-driven mixing of the water column as the lake cools (13). In these lakes, the deepest, densest water is nearer 4 °C, and only a thin layer of water near the surface cools down to near freezing before ice forms. Yang et al. (11) termed the first type of lakes as being "cryomictic," while the second was termed "cryostratified." Not only are the average winter under-ice temperatures different in these two classes of lakes, but the depth of a specific isotherm will be shallower in a cryostratified lake, and deeper in a cryomictic lake (Fig. 1 *A* and *C*). The under-ice thermal structure in lakes can be assessed by the mean ice-on temperature, which is a function of wind speed and lake geometry (11).

One iconic fish that is adapted to ice-covered lakes is Lake Trout (*Salvelinus namaycush*), also known as Lake Charr (14), a lacustrine top predator in cold oligotrophic lakes across Canada and the northern United States (Alaska). Beyond its ecological role, Lake Trout support valuable commercial, recreational, and subsistence fisheries and are therefore a focal species for fisheries management, conservation, and restoration initiatives across much of their range (14, 15). Lake Trout may face increasing physiological stress as climate warming deepens summer thermoclines, reducing the volume of their preferred cold-water habitat in summer; concurrently, oxygen depletion driven by water browning and cultural eutrophication further reduces the volume of suitable habitat in many temperate lakes (16–18). During summer stratification, Lake Trout are found below the thermocline, where they can occupy oxygenated temperatures below 12 to 15 °C that constitute its optimal cold-water habitat (19). Fish habitat selection, however, during the winter ice-covered period is poorly understood (5, 20, 21). This gap raises an interesting and unexplored question: how do Lake Trout respond to different winter thermal stratifications experienced under ice-covered lakes?

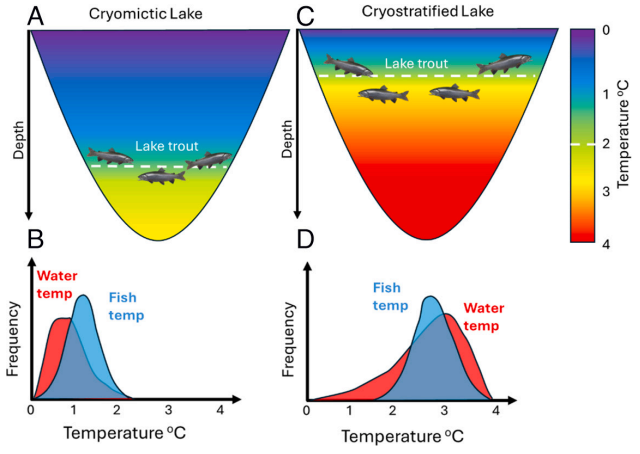

Fig. 1. Conceptual illustration of how lake thermal structure influences winter habitat availability for Lake Trout. A cryomictic lake and a cryostratified lake are distinguished based upon their thermal profile. We hypothesize that Lake Trout occupy a specific range of temperatures ("Goldilocks zone") during winter to minimize the metabolic costs. The depth of this temperature is deeper in cold cryomictic lakes (*A*), with histograms of fish and water temperatures shown in (*B*), and shallower in warmer cryostratified lakes (*C*), with corresponding histograms shown in (*D*). The relative area that Lake Trout can utilize is also smaller in (*A*) compared to (*C*) due to the typical hypsometry of lakes.

Lake Trout are active in winter, exhibiting both movement and feeding behavior so thermal habitat selection is potentially an important element of its winter ecology. Given that the entire thermal range available in winter below ice is only between 0 to 4 °C, finding the optimal winter temperature is a balance; that is, selecting thermal habitat that on one hand conserves energy through reduced metabolic rates while also minimizing physiological stress that may occur with occupancy of temperatures near freezing. Considering food consumption is more temperature-sensitive than metabolism (22), warmer waters could, in theory, enhance energy intake relative to metabolic costs. However, at ice-covered low temperatures, Lake Trout experience relatively reduced mobility and feeding opportunities (21), making energy conservation critical for overwinter survival. Consequently, Lake Trout likely balance restricted energy intake against metabolic expenditure while also avoiding deeper, oxygen-limited waters (18, 19). These considerations raise an important question: do Lake Trout exhibit a "Goldilocks zone" preference in winter, whereby they tend to occupy habitats with temperatures that sufficiently suppress metabolism and conserve energy while avoiding excessive cold stress? Evidence from the related salmonids such as Arctic Charr (*Salvelinus alpinus*) suggests that the cold-adapted species occupy a narrow thermal window, typically between 1 °C and 3 °C, often in the upper, colder water column during inverse stratification (5, 20, 23, 24). These findings suggest that cold-adapted salmonids may exhibit a winter Goldilocks zone, which would be located at temperatures just above the lower lethal limits, i.e., greater than but near 2 °C for Arctic Charr (25, 26). This optimal thermal zone is at very different depths in different lakes. If Lake Trout behave in a similar way to Arctic Charr, we might expect that they are consistently at depths near to the 2 °C isotherm to optimize their metabolism as a survival strategy for winter (27), and that the depth that they use should vary in a predictable way in lakes with different under-ice thermal structures (Fig. 1).

In this paper we aim to determine if the depth that Lake Trout use and preferentially select during winter varies across a gradient of inversely stratified lakes. There are at least ~66,500 Lake Trout lakes in Canada (28) and Alaska (29) (*SI Appendix*, Fig. S1), that have a range of geometries, bathymetries, and wind exposure and hence we expect that the relative depth of the 2 °C isotherm in winter will vary dramatically among them. We use acoustic telemetry data from 11 lakes spanning from 0.3 km^2 to 722.0 km^2 in surface area to estimate Lake Trout depth and thermal habitat use under ice (*SI Appendix*, Fig. S2). Eight lakes have multiple years of data, allowing us to explore interannual variability of the depth of the 2 °C isotherm compared to both mean occupied depth and habitat selection after accounting for depth-specific availability. Finally, theoretical models from Yang et al. (11) and lake data from Minns et al. (28) and Messager et al. (30) were used to predict the degree to which ~66,500 Lake Trout lakes in the North America are closer to cryomictic (nearer 0 °C) or cryostratified (nearer 4 °C) conditions, using 2 °C as the threshold separating these two winter mixing regimes. The same framework was then used to estimate the depths that Lake Trout are expected to occupy during Canadian winters. Results from this study will better inform bioenergetic models at times of the year near metabolic limits of Lake Trout and in turn improve predictions of winter thermal habitat for climate warming projections.

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Results

Physical Processes in Lakes. Observations from 11 lakes reveal substantial variability in ice-on temperature profiles (*SI Appendix*, Fig. S3). In lakes with low geometric aspect ratios (maximum depth to the square root of lake area, $H_{max}/A^{0.5}$~10^{-3}, Dataset S1), i.e., large, shallow-broad systems, such as Lake Simcoe, ice-on temperatures were consistently low across all study years, with volumetrically averaged temperatures remaining below 2 °C. In contrast, lakes with high geometric aspect ratios ($H_{max}/A^{0.5}$~10^{-2}, Dataset S1), i.e., small, deep-narrow systems, exhibited relatively higher ice-on temperatures, with volumetrically averaged temperatures generally exceeding 2 °C. This trend was particularly pronounced in more deep-narrow lakes, such as lakes in the International Institute for Sustainable Development—Experimental Lakes Area (IISD-ELA), Alexie Lake and Lake Papineau, where their separated basins showed vertically averaged ice-on temperatures greater than 3 °C, while near-bottom temperatures approached 4 °C, the temperature of maximum density. Moreover, interannual variability in ice-on temperature profile was evident even within the same lake. For example, in the large, shallow-broad lake, the coldest ice-on temperatures in Lake Simcoe were recorded in 2023 and 2024, with nearly isothermal conditions at ~1 °C. In comparison, the 2022 profiles exhibited ~1.5 °C in the upper water column and ~2 °C near the lake bottom. For smaller, more deep-narrow lakes such as Canoe, Smoke, and Tea Lakes, relatively lower ice-on temperatures were observed in 2024 compared to 2023 or 2022. This is likely due to a delayed onset of ice cover in the warmer 2024, which allowed for prolonged atmospheric heat loss and resulted in lower water temperatures at the time of freezing. A similar thermal response was also observed in IISD-ELA systems (e.g., Lake 223 and Lake 224), where lower ice-on water temperatures occurred in the warmer year of 2024 relative to other years (*SI Appendix*, Fig. S3).

To better understand how ice-on temperatures varied among these lakes, we compared empirical observations with predictive models based on lake geometry. The expanded dataset, which combined 19 global lakes from Yang et al. with the additional 11 lakes included in this study (Eq. **2**, total of 30 lakes) showed a strong linear relationship in log-space (R^2 = 0.58) between ice-on water temperature ($T_{ice\text{-}on}$) and geometric aspect ratios ($H_{max}/A^{0.5}$, Fig. 2*A*). This ratio was higher in smaller, more deep-narrow lakes and lower in large, shallow-broad lakes (Fig. 2*A*). Generally, ice-on temperature was used to distinguish between cryomictic and cryostratified characteristics, with temperatures above 2 °C showing more cryostratified conditions and below 2 °C showing more cryomictic conditions (11). Here, smaller, more deep-narrow lakes tended to have higher ice-on water temperatures and were more cryostratified, whereas the large, shallow-broad lake tended to have lower ice-on temperature and was more cryomictic (Fig. 2*A*). The observed depth of the 2 °C isotherm ($H_{2\,°C}$) was greater in more cryomictic lakes and shallower in more cryostratified lakes. This relationship was well-captured by the strong correlation between the normalized 2 °C isotherm depth ($H_{2°C}/H_{max}$) and geometric aspect ratio (Fig. 2*B*). Additionally, a significant negative correlation was observed between ice-on temperature and the depth of the 2 °C isotherm (Fig. 2*C*), suggesting that lakes with lower ice-on temperatures tend to have a deeper 2 °C isotherm.

The influence of wind speed on ice-on temperature and thermal structure was evident in the strong relationship between surface wind speed (*U*) and the normalized 2 °C isotherm depth (Fig. 2*D*), as well as depth-averaged ice-on temperatures (Fig. 2*E*). This strong relationship suggested that lakes exposed to stronger surface winds before ice-on tend to have a deeper 2 °C isotherm and lower temperatures at ice-on, typically reaching the bottom in larger, more shallow-broad lakes. Conversely, weaker winds lead to a shallower 2 °C isotherm located in the middle-upper water column in smaller, more deep-narrow lakes with higher ice-on temperatures (Fig. 2*E*). These findings suggested that stronger winds drive deeper surface mixing prior to ice-on by delaying ice formation in a larger, more shallow-broad lake, thereby promoting cryomictic conditions. In contrast, weaker wind-driven mixing in smaller, deeper lakes favors the development of cryostratified conditions (11). Furthermore, the depth of the 2 °C isotherm aligned well with the idealized thermocline depth, supporting the usage of the 2 °C isotherm as a representative indicator of the thermocline during the ice-on period (Fig. 2*F*).

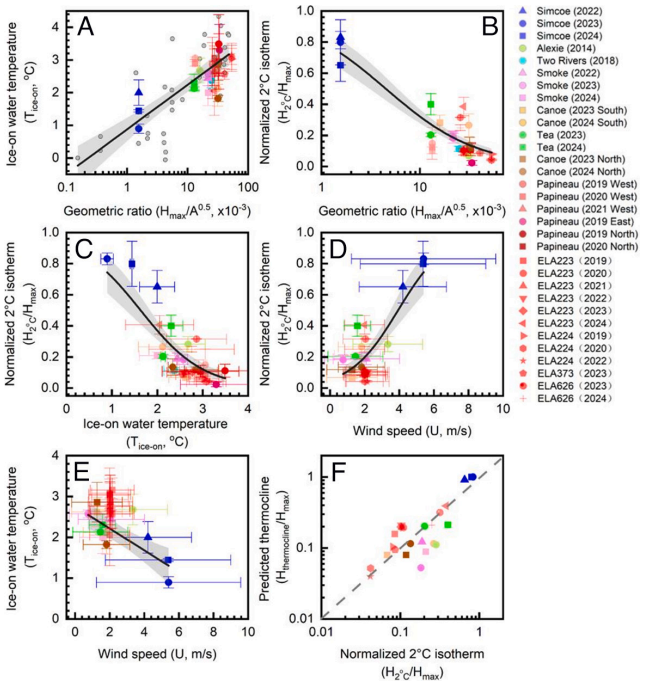

Fig. 2. Influence of lake morphometry and wind forcing on the under-ice thermal structure. (*A*) Ice-on water temperature ($T_{ice\text{-}on}$) vs., the geometric ratio ($H_{max}/A^{0.5}$), where H_{max} is maximum lake depth and *A* is lake surface area. Validation of the lake geometry-based prediction model, which is based on different data sources. Gray points represent the 19 lakes used in Yang et al. (11) from North America, Northern Europe, and Asia; the colored points show the datasets in this study; the black line represents the linear fit based on the combined datasets (R^2 = 0.58). Here also shows the relationships of the normalized 2 °C isotherm depth ($H_{2\,°C}/H_{max}$) to (*B*) $H_{max}/A^{0.5}$, (*C*) $T_{ice\text{-}on}$, (*D*) near-surface wind speed (*U*), averaged over the period from the onset of inverse stratification (cooling to 4 °C) to ice formation. Because $H_{2\,°C}/H_{max}$ is a bounded proportional variable (0 to 1), these relationships were modeled using beta regression with a logit link. Solid curves represent fitted relationships back-transformed to the original scale, and shaded regions indicate 95% CI. (*E*) Relationships between $T_{ice\text{-}on}$ and *U*, modeled using ordinary linear regression following Yang et al. (11). (*F*) Observed $H_{2\,°C}/H_{max}$ compared with predicted values ($H_{thermocline}/H_{max}$) from Eq. **4**. The dashed line denotes the 1:1 relationship, illustrating the correspondence between modeled and observed depth metrics. Point colors represent $T_{ice\text{-}on}$, with red indicating warmer temperatures and blue indicating colder ones. The parameters in the model including linear regression and beta regression with a logit link can be seen in Dataset S3.

Temperature Profiles with Lake Trout Depth Selection During Winter. For smaller, more deep-narrow lakes, such as Papineau, Smoke, Tea, Canoe, Alexie, Lake of Two Rivers and IISD-ELA lakes (Fig. 3 and *SI Appendix*, Fig. S4), higher temperatures were retained before ice forming due to reduced wind-induced mixing. These lakes then had an inverse thermal gradient present under the ice, which was further reinforced due to heat released from bottom

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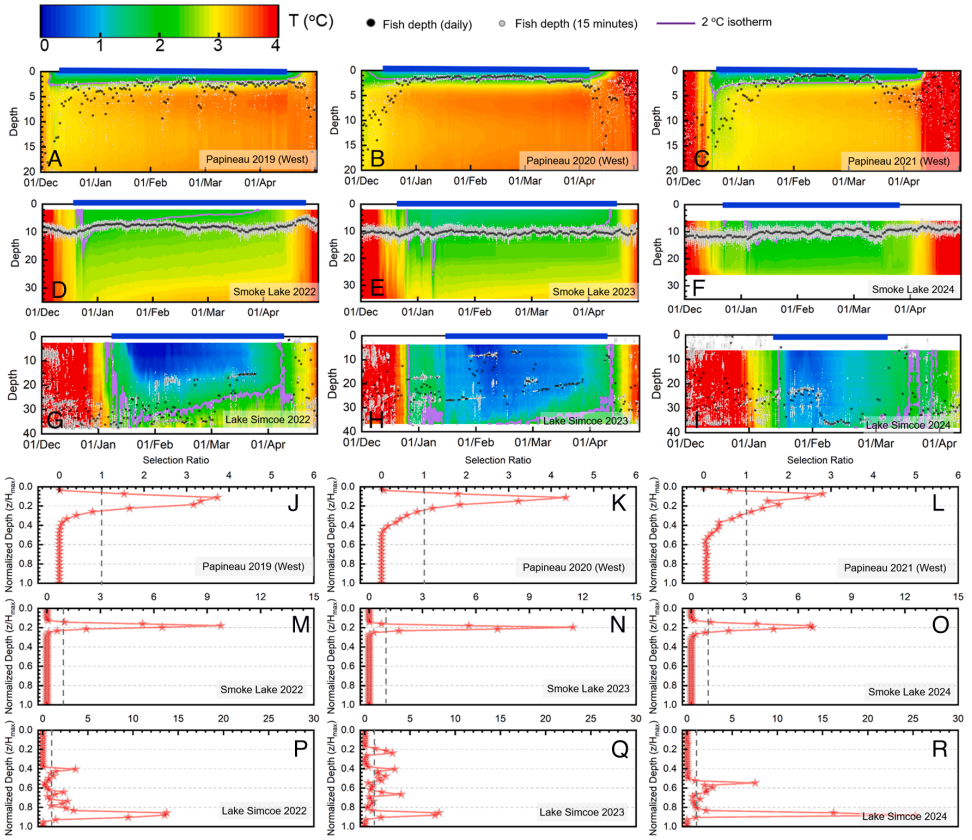

Fig. 3. Observed Lake Trout depth distributions across lakes with different under-ice thermal structures. *Upper* panels (*A*–*I*) show temperature timeseries as a function of depth with the depth use of Lake Trout superimposed. *Lower* panels (*J*–*R*) show selection ratios (SR) profiles, calculated using 1-m depth bins and expressed as a function of normalized depth (z/H_{max}), quantifying depth-specific habitat preference in the water column. This figure shows Lake Trout depth occupancy varies across lakes with different under-ice thermal profiles, ranging from warm to cold systems. Lake Papineau (west), Smoke Lake, and Lake Simcoe are shown here as representative examples, while additional cases are supplemented in *SI Appendix*, Figs. S4 and S5. Note gray and black points in panels (*A*–*I*) represent 15-min and daily averaged depth positions of Lake Trout, respectively, while the purple line denotes the 2 °C isotherm. The top blue bar in panels (*A*–*I*) at each panel represents ice cover. The dashed vertical lines in panel (*J*–*R*) denote SR = 1, where values >1 indicate selection and values <1 indicate avoidance. Across lakes, zones of higher SR consistently occur near the depth of the 2 °C isotherm, indicating a close association between Lake Trout depth distributions and the under-ice thermal structure.

sediments. In these lakes, mid-depth waters often exceeded 2 °C, with bottom temperatures approaching 3~4 °C. Correspondingly, the depth of the 2 °C isotherm in these lakes remained relatively shallow, located within the surface to middle waters (1.14 ± 0.14 m to 11.71 ± 1.20 m; Fig. 3, *SI Appendix*, Fig. S4, and Dataset S4). In contrast, the large, shallow-broad Lake Simcoe (H_{max} = 42 m) exhibited a different thermal structure from 2022–2024, where the top 10 to 20 m of the water column cooled below 1 °C prior to ice formation. Thus, during the ice-covered periods there was a very weak inverse thermal stratification, where the upper half of the water column was less than 1 °C, and between 1 °C and 2 °C near the bottom of the lake. A notable characteristic of this type of lake was the exceptionally deep position of the 2 °C isotherm (purple line, Fig. 3), which was observed at depths of 30 to 40 m (27.3 ± 4.4 m to 33.5 ± 6.1 m) during the ice-covered seasons. Interannual variability also influenced thermal structures in these selected lakes. In Lake Simcoe, for instance, the timing of ice formation was delayed by 1 wk in 2024 compared to 2022, with 2023 falling between the 2 y. The later freeze-up in 2024 led to lower ice-on water temperatures, and the lake exhibited a nearly isothermal structure at lower temperature during the ice-covered period, with the deeper 2 °C isotherm being 33.5 ± 6.1 m (Fig. 3*I*). In contrast, in 2022, a more pronounced inverse stratification developed, with the 2 °C isotherm situated at depths of 27.3 ± 4.4 m (Fig. 3*G*). Similarly, in some small, deep-narrow lakes (e.g., Lake Papineau, Smoke Lake, Canoe Lake, Tea Lake, and IISD-ELA lakes), years with earlier ice freezing led to more pronounced inverse stratification with a shallower 2 °C isotherm (Fig. 3 and *SI Appendix*, Fig. S4).

A key finding is that Lake Trout exhibited distinct depth preferences in lakes with varying inverse thermal structures during ice-covered periods (Fig. 3). When accounting for lake hypsometry (i.e., the depth-dependent distribution of lake volume) using depth-specific selection ratios (SR, i.e., habitat use normalized by volumetric availability), these preferences were consistently aligned with thermally favorable habitats relative to their volumetric availability. In lakes with warmer thermal conditions, Lake Trout preferentially occupied shallower depths. For example, individuals primarily occupied the surface waters in Lake Papineau (west: 3.0 ± 2.3 m to 3.3 ± 0.9 m; east: 3.2 ± 0.8 m; north: 7.9 ± 1.7 m to 8.5 ± 1.2 m), Canoe Lake (north: 0.5 ± 0.7 m to 2.2 ± 2.2 m; south: 5.8 ± 0.6 m to 8.5 ± 0.8 m), and Lake of Two Rivers (3.3 ± 0.5 m), where SR values >1 were concentrated in the upper water column (Fig. 3 and *SI Appendix*, Figs. S4 and S5). Intermediate depth preferences were observed in Smoke Lake (9.9 ± 0.6 m to 10.7 ± 0.5 m), Tea Lake (5.2 ± 0.5 m to 5.7 ± 0.4 m), and Alexie Lake (11.3 ± 0.3 m), corresponding to depth intervals where SR values peaked (Fig. 3 and *SI Appendix*, Figs. S4 and S5). In contrast, in one large lake with colder thermal conditions, Lake Simcoe, Lake Trout occupied much deeper waters (16.8 ± 5.8 m to 26.4 ± 9.6 m) throughout most of the ice-covered season. Peak SR in deep layers indicated that these deep warm waters were preferentially selected to avoid extremely cold surface waters and to optimize their habitat selection to minimize metabolic costs, despite the relatively smaller volumetric availability of these habitats within the lake. However, occasional upward excursions into the mid-to-upper water column (e.g., mid-March 2022 and mid-February 2023) were observed but transient (Fig. 3), likely reflecting short-term ecological drivers, possibly influenced by dissolved oxygen (DO) levels or food availability (*SI Appendix*, Fig. S6). These preferred depth zones in Lake Simcoe corresponded closely to the position of the steep thermal gradient, where the 2 °C isotherm was typically situated.

Lake Trout Thermal Habitat Use. Multiyear water temperature and Lake Trout thermal occupancy across 11 ice-covered lakes revealed distinct habitat use patterns among different lake types (Fig. 4 and *SI Appendix*, Fig. S7). In lakes with relatively warm

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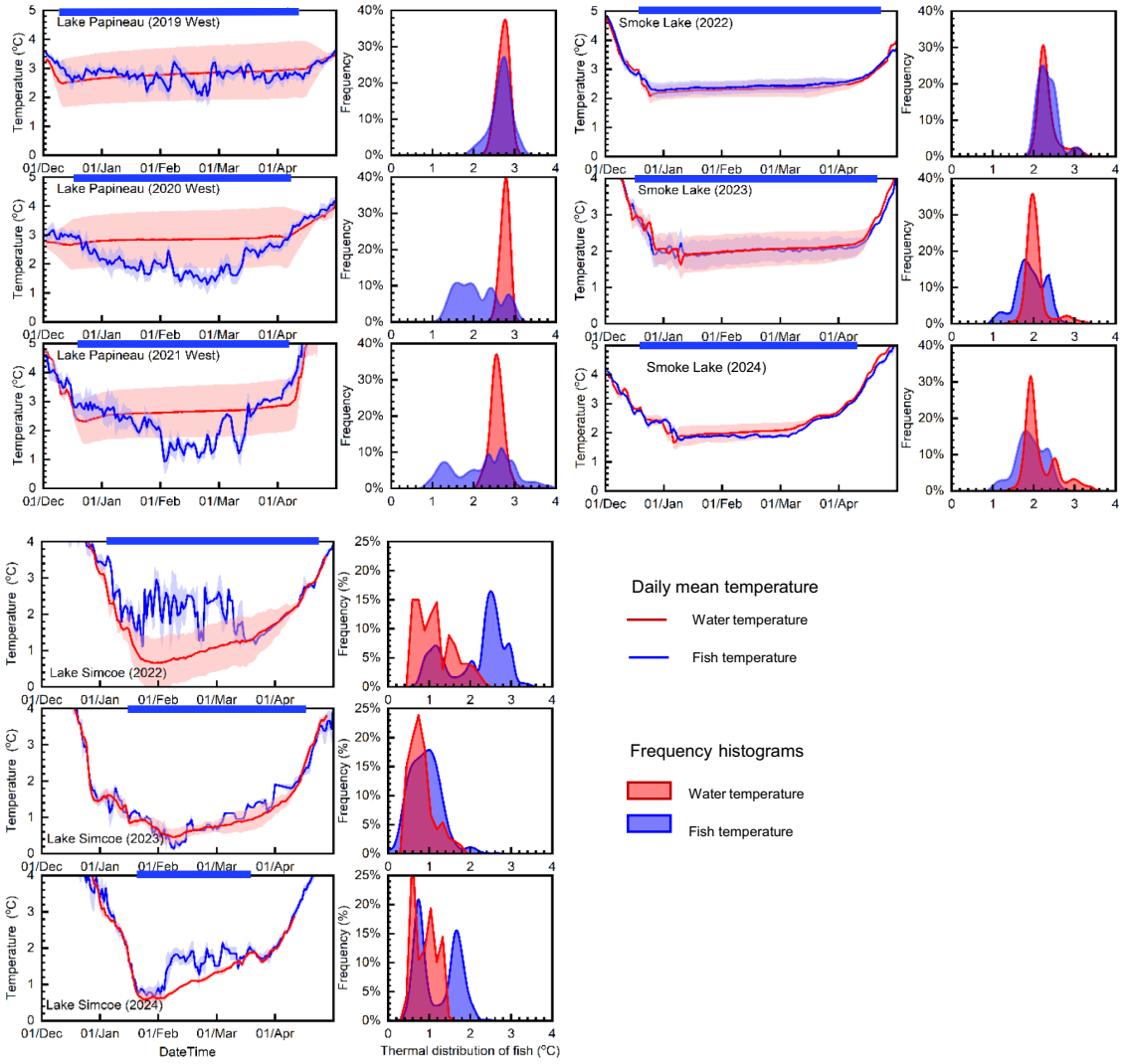

Fig. 4. Comparison of Lake Trout temperatures and available thermal habitat during winter. Plots showing the daily mean temperatures for lake trout (blue) and the volumetrically depth-averaged water temperature (red) during winter. The range of temperatures is indicated by light covering, showing ±SD. The frequency histograms indicate the distribution of available thermal habitat (water temperature; red) in comparison with the temperatures occupied by fish (blue). The blue bar at the top of each panel indicates periods of ice cover. The same plots in other lakes (Papineau North, Papineau East, Canoe South, Canoe North, Lake of Two Rivers, Alexie Lake, Tea Lake, and ELA lakes) are supplemented in *SI Appendix*, Fig. S7. For lakes with individual fish-level temperature data, including Tea, Canoe, and Smoke lakes, Lake Papineau, and Lake Simcoe, these data are supplemented in *SI Appendix*, Fig. S8.

thermal conditions, typically small and deep-narrow systems, Lake Trout occupied similar to or slightly cooler water (2.6 ± 0.6 °C) than the volumetrically depth-averaged water temperature of the lakes (2.8 ± 0.5°C, Fig. 4 and Dataset S4). In most of these lakes (e.g., Lake of Two Rivers, Alexie Lake, Canoe Lake (South), Lake Papineau and IISD-ELA lakes), Lake Trout tended to occupy temperatures lower than the volumetrically depth-averaged water temperature. Frequency distributions further show fish habitat use was concentrated in colder thermal niches in these lakes (Fig. 4 and *SI Appendix*, Fig. S7). Taking Lake of Two Rivers as an example (*SI Appendix*, Fig. S7), the histograms revealed that Lake Trout preferentially occupied 0 to 2 °C waters, despite ambient mean water temperatures predominantly ranging between 2 to 3 °C. However, in some of these lakes with moderately warm thermal structures (Smoke Lake, Tea Lake, and Canoe Lake (North)), the mean temperature occupied by Lake Trout closely followed the variation in volumetrically depth-averaged water temperature (Fig. 4 and *SI Appendix*, Fig. S7), mainly because of reduced thermal gradients within the water column.

In the one large, shallow-broad lake (Lake Simcoe), characterized by colder thermal conditions, the volumetrically depth-averaged water temperature (1.0 ± 0.2 °C, Fig. 4) remained lower during ice-covered periods, which in turn brought about the lower thermal occupancy of Lake Trout (1.5 ± 0.4 °C, Fig. 4). However, interannual variability in thermal habitat use was evident. In some years (e.g., 2022 and 2024), Lake Trout occupied thermal habitats slightly warmer than the volumetric mean during the ice-covered period, with distributions extending toward the upper bound of available temperatures. Thermal habitat use ranged from 1 to 3 °C (mean: 2.1 ± 0.5 °C in 2022; 1.4 ± 0.4 °C in 2024), whereas volumetrically averaged water temperature was lower, ranging from 0 to 2 °C (mean: 1.2 ± 0.5 °C in 2022; and 1.0 ± 0.3 °C in 2024). The thermal occupancy in winter of Lake Simcoe 2023 closely tracked the ambient conditions, with fish thermal occupancy by fish and the volumetric mean being 0.9 ± 0.4 °C and 0.9 ± 0.3 °C, respectively. Frequency histograms across the 3 y in this large, shallow-broad lake consistently show that the peak of Lake Trout thermal habitat use occurred at the upper limit of the mean water temperature (Fig. 4).

Thermal niche breadth also varied systematically with lake type (*SI Appendix*, Fig. S8). In small, deep-narrow lakes, characterized by warmer under-ice thermal conditions (Lake Papineau, and IISD-ELA

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lakes), individual Lake Trout exhibited broader thermal niches, approximately ±2 °C around the daily mean. However, lakes with intermediate thermal structure (e.g., Smoke Lake and Tea Lake) showed more constrained variability (within ±1 °C). The narrowest thermal niches occurred in a large, shallow-broad lake characterized by colder and more weakly stratified conditions, where the temperatures occupied by individual fish fluctuated within ±0.5 °C of the daily mean. This narrow niche likely arose from the limited range of available temperatures in the water column. Although some interannual and among-lake variability was present, the above patterns indicate that thermal niche breadth is primarily governed by the range of available temperatures in the water column, which is influenced by lake morphometry and under-ice thermal structure.

Discussion

Using a unique dataset of fish space use and water temperatures spanning 11 lakes over 32 y, we revealed that Lake Trout exhibited distinct patterns of under-ice habitat use in lakes with different inverse thermal structures. These lakes span a continuum of inverse stratification between the end members of cryostratified lakes with 4 °C mean temperature and cryomictic lakes with 0 °C mean temperature. Lakes with warmer thermal conditions tend to be cryostratified, and fish in these lakes occupied shallow depths (mean fish depth: 0.1 to 11.3 m) with colder winter temperatures (mean thermal habitat use: 2.6 ± 0.6 °C) despite the availability of warmer hypolimnetic habitats (Figs. 3 and 4). Such behavior is likely linked to the strategy of minimizing metabolic costs by selecting the lowest possible temperatures above its lower incipient physiological stressful threshold, while also maintaining access to higher light levels beneath the ice that facilitate visual foraging (21, 31). By contrast, lakes with colder thermal conditions tend to be cryomictic, where the whole water column was below 2 °C, and Lake Trout consistently occupied deeper waters near 1 to 2 °C (mean fish depth: 16.8 to 26.4 m), corresponding to the relatively warmer hypolimnion in cryomictic lakes (mean thermal habitat use: 1.5 ± 0.4 °C, Figs. 3 and 4). This may be due to the necessity for Lake Trout in these colder lakes to seek out warmer thermal habitat to avoid the risk of cold-induced mortality or physiological stress; however, Lake Trout are not able to occupy warmer temperatures in these lakes because of the upper thermal boundary imposed by ambient temperatures. Together, these findings supported our hypothesis that Lake Trout select optimal thermal habitat in winter (i.e., Goldilocks zone preference), such that Lake Trout in the cryomictic lake tended to utilize hypolimnetic waters, but those in cryostratified lakes preferentially exploited shallower waters (Fig. 1). Across all systems, Lake Trout thermal habitat was closely linked to the volumetrically depth-averaged water temperature (*SI Appendix*, Fig. S10, $R^2 = 0.69$). This relationship suggested that Lake Trout primarily occupied the optimal thermal habitat available within each lake, consistent with a habitat-tracking response to lake-specific thermal structure, rather than providing direct evidence of adaptive differentiation among populations.

A key finding of our study is that Lake Trout on average were consistently situated near the depth of the 2 °C isotherm during the ice-covered period (Fig. 3 and *SI Appendix*, Fig. S4). Consequently, variation in the depth of the 2 °C isotherm in different lakes appears to explain much of the interlake variation in winter vertical habitat use (Fig. 5). This was further supported by strong correlations between mean occupied depth and the depth of the 2 °C isotherm ($R^2 = 0.81$, Fig. 5*A*; $R^2 = 0.77$, Fig. 5*B*), which were notably stronger than those observed for the 1.5 °C ($R^2 = 0.59$) and 2.5 °C ($R^2 = 0.58$) isotherms (*SI Appendix*, Fig. S14). However, mean occupied depth alone does not fully distinguish habitat use from habitat preference, because the volume of available habitat changes with depth (32, 33). The strongest evidence for preferential use of the 2 °C thermal zone therefore comes from the selection-ratio analysis, which accounted for depth-specific habitat availability. When habitat use was normalized by volumetric availability, the depth of maximum selection ratio showed an even tighter relationship with the depth of the 2 °C isotherm ($R^2 = 0.93$, Fig. 5*C*; $R^2 = 0.88$, Fig. 5*D*). This result indicates that Lake Trout were not simply occupying depths that were commonly available but were preferentially selecting habitat associated with this thermal boundary. In Lake Simcoe, for instance, individual mean depths mostly occurred deeper than ~40% of the maximum water depth (*SI Appendix*, Fig. S13), indicating consistent use of deeper waters. Although these mean occupied depths did not always fall directly on the 2 °C isotherm, the selection-ratio analysis showed preferential use of the limited, relatively warmer deep-water habitat near the upper end of the available thermal range (Fig. 5 *C* and *D*). In contrast, cryostratified lakes exhibited a shallower 2 °C isotherm and Lake Trout typically occupied and selected shallower portions of the water column (0 to 40%, Fig. 5 and *SI Appendix*, Fig. S13). However, examination of individual data reveals substantial variability in depth use on a daily scale

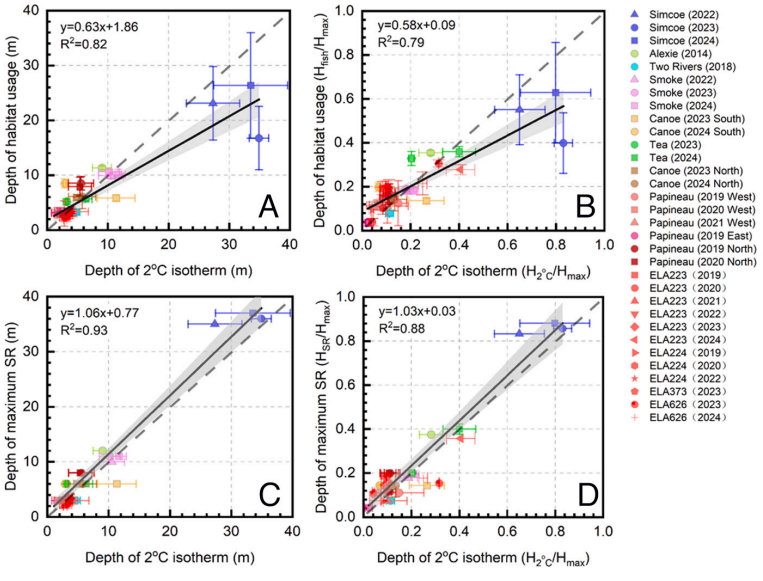

Fig. 5. Lake Trout under-ice mean depth use and availability-corrected habitat selection are associated with the depth of the 2 °C isotherm across lakes and years. (*A*) Mean occupied depth of Lake Trout during the ice-covered period, plotted against the depth of the 2 °C isotherm, with error bars indicating SD. (*B*) Same as (*A*), but depth is normalized by the maximum depth of each lake. (*C*) Depth corresponding to the maximum selection ratio (SR) of Lake Trout plotted against the depth of the 2 °C isotherm, with error bars indicating variability. (*D*) Same as (*C*), with depths normalized by maximum lake depth. The diagonal dashed line represents a 1:1 relationship. Strong positive correlations in panels (*A* and *B*) indicate that the depth of the 2 °C isotherm is a robust predictor of Lake Trout winter habitat use and, more strongly, winter habitat selection when accounting for volumetric availability in panels (*C* and *D*). The relationship between individual-level fish depth and the depth of the 2 °C isotherm is further supplemented in *SI Appendix*, Fig. S12. In addition, the plots of fish depth use in relation to the depths of the 1.5 °C and 2.5 °C isotherms are supplemented in *SI Appendix*, Fig. S13. Among these comparisons, the correlation with the 2 °C isotherm was the strongest, further confirming that the 2 °C isotherm provides the strongest correspondence with Lake Trout habitat use in winter.

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(*SI Appendix*, Fig. S9), indicating that factors beyond temperature can influence short-term fish habitat use. Dissolved oxygen (DO) was one such factor that acted jointly with temperature to define the oxythermal niche (19, 27, 34). For example, Lake Trout occasionally occupied shallower depths than the 2 °C isotherm in Lake Simcoe (2022 and 2023, *SI Appendix*, Fig. S6), likely avoiding low-oxygen bottom waters (<7 mg/L), a threshold associated with optimal Lake Trout habitat suitability (27). The effects of DO constraints on fish habitat use were also observed in some cryostratified systems (e.g., Tea Lake; *SI Appendix*, Fig. S6). However, DO was generally not a primary limiting factor, because most systems exhibited sufficiently high oxygen concentrations throughout the water column (*SI Appendix*, Fig. S15), with volume below 7 mg/L comprising a small fraction of total volume (typically <10% of volume weighted habitat; Dataset S5). While fish habitat depth against the 7 mg/L isoline on daily scale indicated individual fish responded to oxygen variability, the correlation on average remained weak (R^2 = 0.13, *SI Appendix*, Fig. S16), suggesting that DO was a weaker predictor of winter habitat use than temperature at the cross-lake scale, at least for the lakes in this study. Light and other behavioral drivers (e.g., foraging) may also contribute to short-term deviations from thermally optimal depths (21, 35, 36). However, during winter the impact of light levels on Lake Trout depth, swimming speed, and nearshore habitat use were less clear due to short day length and ice–snow cover (21). Taken together, these observations indicated that while individual Lake Trout exhibited considerable short-term behavioral variability, their time-averaged depth use was broadly associated with the 2 °C isotherm, and their availability-corrected habitat selection was even more strongly linked to this thermal boundary across lakes. The depth of the 2 °C isotherm provides a robust cross-lake predictor of winter habitat selection.

Given the nonlinear decrease in lake area with depth, the volume of water available for Lake Trout was more limited at deeper layers. Bathymetric analysis indicated that, in a cryomictic (Lake Simcoe), the available area that Lake Trout could utilize across the 2 °C isotherm ranged from 28 to 37% of the lake surface area, and the corresponding volume below the 2 °C isotherm comprised only 5 to 18% of the total lake volume during the winters of 2022–2024 (Dataset S5). This limited area and volume implied that Lake Trout in the large cryomictic lake occupied a relatively constrained space, which was consistent with the previous telemetry studies showing reduced winter habitat use (20, 21). In those studies, a compression of available habitat may cause fish densities per unit volume of usable habitat to increase and thus more pressure can occur on food resources, much as they do during the open water season as summer progresses (16, 19). In cryostratified lakes, a larger relative area and proportion of the lake volume was within their preferred thermal range. For these lakes, the relative available area accessible to Lake Trout across 2 °C isotherm ranged from 38 to 99% of the surface water layer, and the corresponding volumetric availability ranged from 27 to 92% (Dataset S5). These findings suggest that variation in available Lake Trout habitat during winter arises from the variations in the thermocline depth and associated hypsometric constraints; deeper thermoclines compress cold-water habitat into a smaller hypolimnetic volume, increasing spatial constraints and potential intraspecific competition, whereas shallower thermoclines allow for more extensive and accessible thermal habitat.

To place these findings in a broader geographic context, we extended our analysis across Lake Trout lakes in Canada and Alaska, regions that contain the largest number of lakes globally (37) and support rich freshwater fisheries resources. For example, the province of Ontario in Canada contains over 250,000 lakes; only about 1% of these lakes (~2,300) are known to support Lake Trout populations, but account for approximately 20 to 25% of all Lake Trout lakes globally (38). To estimate the potential winter temperatures in Lake Trout lakes across Canada and Alaska, we used the geometry-based predictions of ice-on temperatures (11) with our data on Lake Trout distributions in these regions (Fig. 6*A*). We found that lakes with higher predicted ice-on

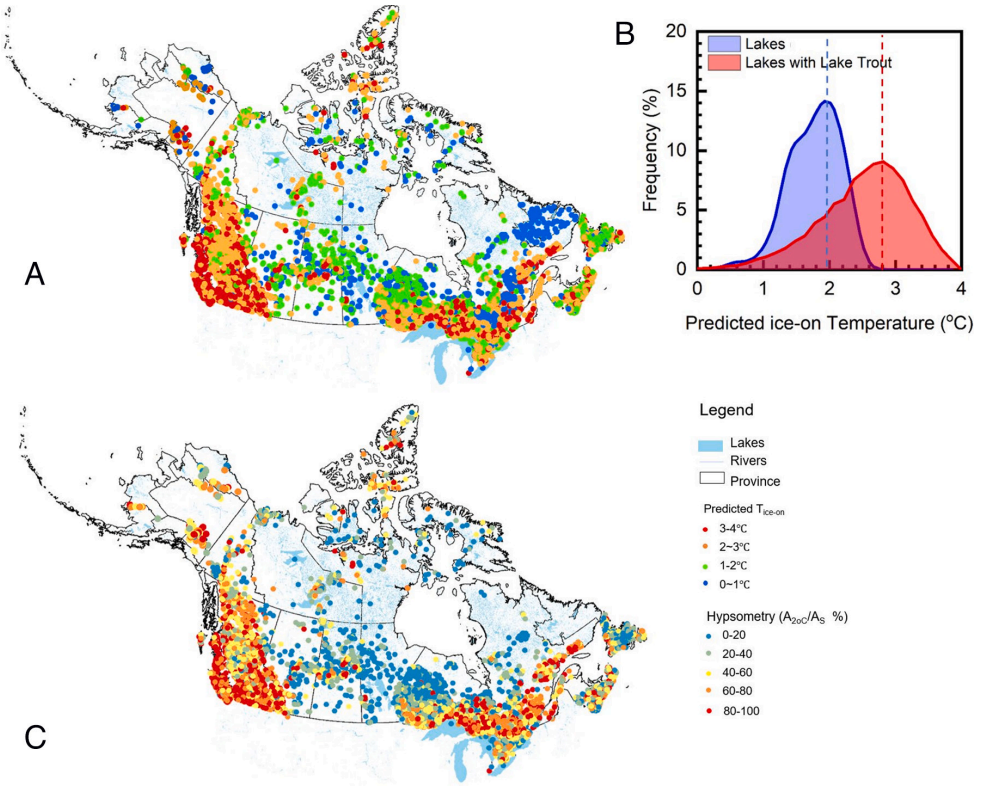

Fig. 6. Spatial patterns of predicted ice-on temperature and associated winter thermal habitat availability across lakes in Canada and Alaska. (*A*) A map of Canada and Alaska with predicted depth averaged ice-on lake temperature (T_{iceon}) distribution based on geometric ratio for the lakes known to support Lake Trout. (*B*) Frequency histograms of predicted ice-on temperatures for all Canada lakes (blue) and for Lake Trout bearing lakes (red), showing distinct thermal distributions across lake types. (*C*) A map of Canada showing the predicted ratio of the cross-sectional area intersected by 2 °C isotherm ($A_{2°C}$) to the surface area (A_S) during the winter ice-covered period. This metric reflects the effects of lake hypsometry on the area of habitat available to Lake Trout in winter. Smaller values indicate that the deeper their preferred habitat is, the less area available, and the more pressure there is on food resources as the density of fish increases. The normalized 2 °C isotherm depth (expressed as the ratio $H_{2°C}/H_{max}$) was estimated based on geometric ratio. The predicted proportion of lake water volume located below the 2 °C isotherm are supplemented in *SI Appendix*, Fig. S14. Note that the map shows much fewer lakes than exist in the Canada and Alaska.

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temperatures (i.e., >2 °C, cryostratified) were concentrated in the southern regions of Canada (Fig. 6*A*), including southern British Columbia, Alberta, Ontario, and Quebec, as well as parts of the Atlantic provinces, while colder lakes (<2 °C, cryomictic) in winter were predominantly distributed across northern and high-latitude regions (Fig. 6*A*), such as the Yukon, Northwest Territories, Nunavut, and the northern portions of Manitoba, Saskatchewan, Ontario, and Quebec. This geographic division aligns closely with the Canadian Shield (*SI Appendix*, Fig. S1*C*). Lakes in northern Canada tend to be shallower and situated on tundra landscapes, thus are more likely to be cryomictic. Based on our classification, 56% of all selected north American lakes (877,927 lakes) were identified as cryomictic and 44% as cryostratified. Among lakes supporting Lake Trout (66,500 lakes), the proportion of cryostratified systems was much higher (27% cryomictic vs. 73% cryostratified; Fig. 6*A*), indicating that Lake Trout were preferentially associated with warmer thermal conditions under ice.

These cryostratified lakes typically exhibited a larger cross-sectional area across the preferred 2 °C thermal habitat zone (Fig. 6*C*), where Lake Trout selection was strongest (Fig. 5), thereby providing more extensive thermal refuge and foraging space for Lake Trout. In contrast, cryomictic lakes had a much smaller relative area of the 2 °C habitat occupancy (Fig. 6*C*), thus offering limited habitat availability for cold-water species. Specifically, Lake Trout lakes in southern Ontario (Fig. 6*A* and *SI Appendix*, Fig. S1 *B* and *C*), were generally cryostratified systems, with the relative area of the preferred 2 °C thermal habitat zone exceeding 40%, while the northernmost parts of Ontario, especially those situated across the Canadian Shield, were cryomictic, with the relative area of the 2 °C habitat occupancy less than 20% (Fig. 6*C*). In western Canadian provinces and territories where Lake Trout was relatively abundant, such as British Columbia, Alberta, and the Yukon, most lakes were cryostratified (Fig. 6*A*) and a relatively large cross-sectional area (>40%, and often >60%) was occupied by the 2 °C habitat zone (Fig. 6*C*). Taken together, these results presented a valuable framework for evaluating thermal habitat accessibility across different lake types: Lake Trout in cryostratified systems tended to occupy mid-to-upper water column (Fig. 1*C*), where thermal refuge was abundant (>60% of area), while Lake Trout in cryomictic lakes inhabit deeper waters (Fig. 1*A*), where suitable habitat was limited (<40% of area), possibly increasing ecological pressures on cryomictic populations during winter. Compression of fish within a narrow vertical habitat range could make them more vulnerable to harvest by fishers with sonar technology, readily available and used today. This classification system could serve as a cost-effective and scalable tool for informing the vulnerability of cold-water fisheries in management decisions made by agencies and organizations responsible for the sustainability of the resource.

Comparative analysis of Lake Trout thermal habitat use and body sizes across all-type lakes revealed a negative relationship between individual thermal habitat use and body size (*SI Appendix*, Fig. S11). However, given substantial differences among lakes in thermal regimes, morphometry, and food web structure, these environmental factors likely interact to shape Lake Trout population size structure and growth patterns. Importantly, despite more limited thermal habitat (i.e., reduced volume below the 2 °C isotherm, Dataset S5) in cryomictic lakes, Lake Trout in Lake Simcoe attained larger sizes than in cryostratified systems (*SI Appendix*, Fig. S11), indicating that such physical constraints do not necessarily translate into reduced individual growth or body size, but instead might be a result of trophic structure (39, 40). In addition, cryostratified lakes typically offer relatively warmer environments, whereas cryomictic lakes provide colder habitats (Fig. 4 and *SI Appendix*, Fig. S7). If fish are behaviorally thermoregulating by actively seeking their preferred thermal habitats in winter, as our results suggest, this behavior may involve trade-offs between thermal optimization and energetic costs (26, 41). In cryostratified lakes, occupying warmer habitats could slightly increase metabolic demand, possibly reducing energy allocation to growth and reproduction, which potentially contribute to smaller body sizes observed in some cryostratified system (*SI Appendix*, Fig. S11). Nevertheless, thermal habitats may not be sole contributor to fish body size; the availability of high-energy prey resources [e.g., Cisco (*Coregonus artedi*) and Rainbow Smelt (*Osmerus mordax*)] that could enhance growth efficiency is also a key factor. The presence and abundance of these forage fishes differ among lakes (Dataset S1). In our cryomictic lake (Lake Simcoe), Lake Trout primarily consume pelagic forage fishes such as Yellow Perch (*Perca flavescens*), Cisco, and Rainbow Smelt (42), whereas in many cryostratified lakes diets include a greater proportion of invertebrate species (21, 26, 43, 44). Lake Trout populations that feed at higher trophic levels (i.e., primarily on fish rather than invertebrates) are generally associated with greater growth efficiency and larger adult body sizes (45, 46). However, such trophic specialization is often associated with lower population biomass and abundance (47, 48), although most available diet data are derived from the open-water season and winter feeding remains poorly understood, with potential seasonal shifts in prey use (21, 49). Consequently, we do not have direct winter data on population size, biomass, or harvest rates to evaluate this in our study lakes.

Under ice-covered conditions, Lake Trout may face trade-offs between selecting thermally optimal habitats and accessing sufficient prey resources. As a winter-active species, they may gain metabolic advantages by occupying specific temperature ranges, but this might also come at a cost of reduced access to prey in certain lakes or years. Unfortunately, the lack of winter prey density and distribution data prevents a more detailed assessment of this trade-off. When examined separately by lake type, our findings indicate that in the cryomictic lake, Lake Trout body size was negatively associated with thermal habitat use; smaller individuals select relatively warmer waters, while larger individuals occupy colder waters (*SI Appendix*, Fig. S11), a pattern observed for salmonids during periods of lake or marine stratification (50). This pattern may reflect the inverse relationship between body size and optimum temperature of net energy gain (51). If so, our results suggest that during winter, the optimum temperature available for net energy gain has shifted to colder temperatures relative to temperatures experienced by lake trout during summer stratification. Meanwhile, deeper thermoclines and limited volume below the 2 °C isotherm in cryomictic systems restrict preferred habitat to narrow, deeper layers with potentially heightened competition for resources, which can be accessed more effectively by larger individuals with greater physiological capacity (5). On the other hand, physiological constraints may also play a role, as larger Lake Trout are better able to withstand colder waters, where lower metabolic rates reduce energy expenditure. By contrast, cryostratified lakes feature shallower thermoclines and a broader volume within the 2 to 4 °C thermal refuge, providing more expansive and accessible habitat. Under such conditions, environmental pressure is reduced and Lake Trout can occupy a wider range of depths regardless of body size, resulting in a weaker relationship between individual size and thermal habitat (*SI Appendix*, Fig. S11).

Thermal habitat heterogeneity may also influence habitat selection within lakes, particularly in complex or multibasin systems such as Canoe Lake and Lake Papineau. In these systems, differences in geometric aspect ratio significantly affect ice-on timing (Fig. 2*A*), which in turn shapes the under-ice inverse thermal

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structure and determines the depth of the 2 °C isotherm (Fig. 2*B*). For example, subbasins such as Canoe Lake South and Lake Papineau North with larger geometric ratio exhibit higher ice-on water temperatures, leading to a more pronounced inverse thermal gradient during ice cover. These steep gradients occurred closer to the surface, thereby promoting more consistent and accessible thermal habitat usage by Lake Trout. In contrast, other regions within these same lakes, characterized by lower geometric ratio, display deeper thermal step gradients (Figs. 2*B* and 3), which would consequently reduce the thermal habitat available for Lake Trout. Moreover, intralake differences in access to suitable thermal habitats may influence individual energetic costs associated with foraging and habitat selection (26). In lakes with pronounced bathymetric fragmentation or topographic complexity (e.g., Canoe and Papineau lakes), Lake Trout should expend more energy in locating favorable thermal and oxygen conditions. Conversely, in morphometrically simpler or smaller systems (e.g., Tea Lake and Lake of Two Rivers), prey and habitat may be more spatially concentrated, potentially reducing energy expenditure (26).

As the phenology of water temperature varied interannually, Lake Trout exhibited corresponding adjustments in habitat usage across both lakes with varying under-ice thermal structures. For instance, in Lake Simcoe, the ice cover in 2024 was thinner and much delayed compared to 2022. This delay in lake surface freezing weakened the inverse thermal stratification, leading to more vertically mixed conditions prior to ice formation (Fig. 3 and *SI Appendix*, Fig. S4). Consequently, the 2 °C isotherm, which was located at ~30 m in 2022, deepened to ~40 m in 2023 and even reached the lake bottom in 2024, effectively erasing optimal winter thermal refuge for Lake Trout. The mean under-ice water temperature was also lower in 2024, forcing Lake Trout to adjust its most selected thermal habitat downward and habitat usage to deep positions (Fig. 3 and *SI Appendix*, Fig. S4). Similar patterns were observed in Algonquin small lakes (2024) and Lake Papineau (2021), where reduced ice thickness and shorter ice duration coincided with weaker inverse stratification. In these systems, the depth of the steep thermal gradient increased during such years, pushing fish habitat use toward deeper waters (Fig. 3 and *SI Appendix*, Fig. S4). These findings suggested that while the influence of winter thermal phenology on Lake Trout habitat selection appears consistent across different lake types, the magnitude of this effect may vary depending on lake morphology.

Against the backdrop of ongoing climate warming, lake ice phenology was undergoing significant changes, with freeze-up events generally occurring later, which may allow a longer period of wind-driven fall mixing and heat loss before ice formation, so that the water column can cool more before ice-on (16, 52). This trend may cause cryostratified lakes to transition toward cryomictic regimes, which would deepen the 2 °C isotherm, constraining overwintering habitat availability for cold-water species. However, global projections suggested that such thermal regime shifts remain relatively limited, with only ~0.1 to 1% of lakes expected to transition under Representative Concentration Pathways (RCPs) 2.6 to 8.5 scenarios (53), indicating that additional controls modulate this response. Previous studies demonstrated that lake morphometry and wind speed are the most important predictors explaining the across-lake variation in the winter mixing regimes (11, 53). The strong relationship between wind speed and ice-on temperature (Fig. 2*E*) suggests a critical threshold at ~2.9 m/s, corresponding to the threshold temperature of 2 °C separating cryostratified from cryomictic conditions (11). This threshold is consistent with the regression tree analysis of Woolway et al. (53), indicating that lakes exposed to higher wind speeds ≥2.9 m/s are predominantly cryomictic. In contrast, in calm regions (<2.9 m/s), lake morphometry sets the baseline thermal structure, with wind forcing modulating this baseline and governing interannual variability in ice-on temperature and mixing regimes. Lakes in calmer regions can also be cryomictic if the lake geometric ratio is relatively small (Fig. 2*A*), cryostratified lakes are more commonly associated with low wind exposure and deep-narrow morphometry. Near-surface wind speeds could weaken winter thermal stratification and deepen the 2 °C isotherm by delaying ice formation or disrupting already-formed ice cover (54). This is supported by the positive relationship between wind speed and the normalized 2 °C isotherm depth (Fig. 2*D*), although regional wind trends may differ between large exposed lakes and smaller sheltered systems (55, 56). Increasing wind speeds are therefore expected to promote cryomictic conditions in larger, shallow-broad lakes, deepening the 2 °C isotherm and compressing thermal refuge for cold-water species. Conversely, decreasing wind speeds may favor cryostratified states in small, deep-narrow lakes, thereby expanding thermally suitable habitats and foraging opportunities for Lake Trout. Together, these findings highlight the importance of considering both morphometry and varying climate forcing, especially wind speed, when predicting future winter habitat availability for Lake Trout. More broadly, shifts in under-ice thermal habitat are directly relevant to conservation and management, because Lake Trout are cold-water top predators and support important commercial, recreational, and subsistence fisheries across much of their range (14, 15). The depth of the 2 °C isotherm provides a transferable indicator of winter habitat availability and potential habitat compression, complementing existing assessments that focus largely on summer oxythermal habitat (27, 57). Incorporating winter thermal habitat into lake-specific management frameworks could improve predictions of Lake Trout responses to changing ice cover and climate-driven thermal regimes (58), and therefore help refine growth and harvest models that are used to implement sustainable harvests of our valuable cold-water fisheries (14).

Materials and Methods

Overview. There are over 2,000,000 lakes in Canada and Alaska, constituting around 14% of the lakes in the world (59). Of these, geospatial data for 877,927 lakes were obtained from the HydroLAKES database (30), which provides comprehensive hydrographic morphometric information, including lake location, surface area, shoreline length, mean, and maximum lake depth (*SI Appendix*, Fig. S1). Information specific to Lake Trout habitats was extracted from the designated Lake Trout lakes inventory from the Ontario Ministry of Natural Resources (60) and for other regions in Canada (28) and Alaska (29), enabling identification of lakes that support Lake Trout populations and characterization of their geomorphometry. Among them, an estimated 66,500 are Lake Trout lakes, spanning approximately 3,510,000 km^2, primarily located in south central Canada, within the Boreal and Taiga Shield ecozones (28). These lakes comprise the majority of all native Lake Trout lakes globally. Winter thermal regimes of the selected North American lakes were estimated by applying lake geometry-based predictions of ice-on temperatures (11). This approach enabled us to classify individual systems as either cryostratified or cryomictic, thereby informing the potential overwinter thermal habitat available to Lake Trout.

To investigate Lake Trout thermal habitat selection across different lake types during ice-covered periods, we utilized continuous acoustic telemetry data in combination with vertical temperature profiles from 11 lakes over multiple years (*SI Appendix*, Fig. S2). These included a large, shallow-broad lake, i.e., Lake Simcoe (61), and a series of small, deep-narrow lakes, i.e., Alexie Lake (21), Lake of Two Rivers (43), Smoke Lake, Tea Lake, Canoe Lake (44), Lake Papineau (26), and four lakes within the International Institute for Sustainable Development (IISD)-Experimental Lakes Area (ELA) (Lake 223, Lake 224, Lake 373, and Lake 626) (45, 62). Notably, Canoe Lake and Lake Papineau comprise two and three relatively discrete subbasins, respectively, which are connected by narrow, shallow channels (100 to 250 m wide, ≤10 m deep). These interbasin connections may

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act as physical (e.g., ice) and thermal (step gradient) barriers potentially limiting fish movement between basins (*SI Appendix*, Fig. S2). Detailed lake morphometric characteristics and sampling protocols are provided in Dataset S1 and S2. Acoustic telemetry data were used to calculate both depth and thermal preferences of each species, and thermal profile datasets were used to quantify the magnitude of thermal habitat change under ice-covered conditions. The selected lakes span a wide range of surface areas (0.3 to 722.0 km^2) and maximum depths (13 to 90 m) (*SI Appendix*, Fig. S2 and Dataset S1). Their dimensionless morphometric ratios ($H_{max}/A^{0.5}$, i.e., maximum depth to the square root of lake area) vary from 1.6×10^{-6} to 5.3×10^{-2}, allowing us to categorize them into cryostratified or cryomictic types based on their geometry-driven ice-on temperature regimes (11).

Lake Temperatures and Habitat Use. Water temperatures in all study lakes were measured at multiple depths using strings of thermal loggers (Dataset S2). Temperature logger strings were not extended to the lake surface to prevent damage from ice, with the shallowest thermistors typically deployed at depths of 0.5 to 2 m. Given that Canoe Lake and Lake Papineau each comprise two and three relatively independent subbasins, respectively, one temperature logger string was installed in each subbasin. Since temperature monitoring was carried out by different personnel across lakes, the measurement interval (i.e., sampling frequencies) varied. To ensure consistency across datasets, we standardized the presented temperature profile data by computing 15-min and daily averages. This standardization was applied to all lakes except Lake of Two Rivers and Alexie Lake, which were monitored at a daily frequency. The measured water temperature profiles were primarily used to assess the thermal habitats available within each lake basin. Ice-on and ice-off dates for all 11 lakes were obtained from multiple data sources (*Data, Materials, and Software Availability*). Out of the 11 study lakes, 9 (Alexie, Smoke, Tea, Canoe, four IISD-ELA lakes, and Lake Simcoe) included hourly wind speed measurements at the nearest meteorological site.

The 11 study lakes were instrumented with networks of acoustic receivers. Fish were surgically implanted with acoustic tags equipped with pressure sensors that transmit individual identifications as well as their depth. Many of the acoustic receiver stations also had companion temperature recorders so that the thermal conditions of each lake can be estimated at time scales that are matched to fish movements. The number of tagged fish, acoustic receivers, and transmitter deployments varied by lake; these details are summarized in *SI Appendix, Text S1* and Dataset S2. Raw telemetry data were filtered prior to analysis (*SI Appendix, Text S2*). Depth and temperature data from tagged Lake Trout were averaged at 15-min and daily intervals to align with the corresponding water temperature datasets, facilitating cross-comparison between fish behavior and thermal habitat conditions in each lake.

Definition of Cryostratified and Cryomictic Lakes. For the 11 specific lakes selected in our study, depth-averaged water temperatures were calculated at the time of reported ice-on. A surface water temperature of 0 °C was assumed at z = 0 m, and linear interpolation was applied between this assumed value and the shallowest measured temperature. To predict the ice-on water temperatures for many other northern lakes, where there were no vertical temperature profile measurements from thermistor chains, we modified a lake-geometry-based predictive model developed by Yang et al. (11). This model is based on a strong empirical linear relationship observed between depth averaged ice-on temperature ($T_{ice\text{-}on}$) and the geometric parameter $\log_{10}(H_{max}/A^{0.5})$, fitting across 19 lakes in North America, Northern Europe, and Asia, was expressed as

$$T_{ice-on} = 5.50 + 1.59 \times log_{10}\left(H_{max}/A^{0.5}\right). \quad [1]$$

We extended this relationship by including observations from the 11 additional lakes analyzed in this study (30 lakes, Fig. 2*A*), resulting in a modified empirical equation:

$$T_{ice-on} = 4.97 + 1.37 \times log_{10}(^{H_{max}}/_{A^{0.5}}). \quad [2]$$

We applied this model to estimate ice-on temperatures for additional lakes across Canada and Alaska (Fig. 6*A*). It was noted that uncertainty in this empirical model ($R^2 = 0.58$) introduces variability in predicted ice-on temperatures, particularly for lakes with predicted temperatures near the ~2 °C threshold, where classification is less certain.

To better understand the abundance and behavior of fish across different lake types, we categorized our study lakes according to the thermal categorization scheme of Yang et al. (11), where ice-covered lakes are separated into cryomictic and cryostratified lakes. Lakes with higher $H_{max}/A^{0.5}$ values, i.e., a smaller surface area relative to depth, are considered cryostratified (11). These lakes are generally less wind-exposed in winter and tend to develop thermal stratification beneath the ice, exhibiting relatively warmer under-ice conditions, with depth-averaged temperatures typically between 2 °C and 4 °C. In contrast, lakes with lower $H_{max}/A^{0.5}$ values, usually larger and shallower, are classified as cryomictic. These lakes experience stronger surface winds that may delay ice formation and promote extended mixing, resulting in colder, more isothermal temperature profiles at ice-on, typically ranging between 0 °C and 2 °C (11, 53). Furthermore, by applying the lake geometry-based predictions of ice-on temperatures, which define approximate characteristic temperature ranges for cryostratified (2 to 4 °C) and cryomictic (0 to 2 °C) lakes, additional lakes across Canada and Alaska can be classified into these two winter mixing regimes, even in the absence of direct under-ice temperature measurements.

Selection Ratios and Habitat Volume. To quantify depth-specific habitat preference while accounting for lake hypsometry effect, selection ratios (SR) were calculated as the ratio of habitat use to availability (33), expressed as

$$SR = {}^{u_{i+}}/_{(\pi_i u_{++})}, \quad [3]$$

where u_{i+} is the number of fish observations in depth bin i, u_{++} is the total number of observations, and π_i is the proportion of available habitat, estimated from bathymetry-derived volume within each 1-m depth interval. This approach allows habitat use to be evaluated relative to volumetric availability across the water column, where SR > 1 indicates preference for the given depth, whereas SR < 1 indicates avoidance for that particular habitat (32, 33, 63).

Once selection has been established, we estimate the available habitat volume of Lake Trout during winter ice-covered periods by quantifying the depth of the thermocline, as it defines the vertical position of key thermal boundaries (e.g., the 2 °C isotherm) and thus constrains the accessible volume to Lake Trout. According to thermocline scaling proposed by Gorham and Boyce (1989) (64), the thermocline depth is mainly determined by lake geometry and by shear-induced mixing, which is driven by the fundamental internal seiche in small lakes and by near-inertial motions in large lakes. This framework aligns with previous studies on the mixing dynamics in stratified lake on behalf of a Wedderburn number (65). Similar to ice-on water temperatures estimated above, the thermocline depth prior to the time of ice-on can be estimated using lake morphometry and wind forcing (11), and is expressed as

$$H_{thermocline} = 2 - \left(\frac{u_*^2}{g'}\right)^{0.5} A^{0.25}. \quad [4]$$

The reduced gravity (g′) is defined based on the density difference between water at 0 °C and 4 °C as $g' = g(\rho_{4^oC} - \rho_{0^oC})/0.5(\rho_{4^oC} + \rho_{0^oC})$, where g is the acceleration due to gravity, and $\rho_{0\,°C}$ and $\rho_{4\,°C}$ represent the densities of water at 0 °C and 4 °C, respectively. The overbar $\bar{}$ denotes temporal averaging from the onset of inverse stratification to the formation of ice. Because the 2 °C isotherm typically aligns with regions of steep thermal gradients under ice cover (11), we approximated the depth of the thermal step gradient using the depth of the 2 °C isotherm in our analysis, i.e., $H_{2^oC} \approx H_{thermocline}$.

Variations in the depth of this thermocline lead to a changing volume of cold-water habitat available to Lake Trout. A deeper winter thermocline implies that only a smaller volume of optimal habitat remains below this temperature threshold, reducing the habitable space available to fish and increasing intraspecific competition for food resources (16). These effects of lake hypsometry on habitat availability are thus essential for the ecological constraints on cold-water fish species. To quantify this, we used bathymetric data to calculate the ratio of the cross-sectional area intersected by 2 °C isotherm to the surface water area, as well as the proportion of lake volume below the winter thermocline for 11 representative lakes over a 32-y period (*SI Appendix*, Text S3 and Dataset S5). Furthermore, we applied a strong empirical relationship between $H_2{}^oC/H_{max}$ and $H_{max}/A^{0.5}$, derived from these 11 lakes with 32-y datasets, to estimate cross-sectional area and the proportion of deep-water volume across Canadian and Alaskan lakes. This estimation was based on the assumption of a simplified triangular lake geometry (66). Details of the method are provided in *SI Appendix, Text S3*, and the resulting spatial estimates are shown in Fig. 6*C* and *SI Appendix*, Fig. S17.

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Data, Materials, and Software Availability. The high-frequency water temperature and acoustic telemetry datasets used in this study, covering 11 lakes (Lake Simcoe, four Experimental Lakes Area lakes, Smoke Lake, Tea Lake, Canoe Lake, Lake Papineau, Lake of Two Rivers, and Alexie Lake), are publicly available via Zenodo (https://zenodo.org/records/23527207) (67). Geospatial data for lakes across Canada and Alaska were obtained from the HydroLAKES database (https://www.hydrosheds.org/products/hydrolakes) (68). Information specific to Lake Trout habitats was extracted from the designated Lake Trout lakes inventory from the Ontario Ministry of Natural Resources (https://www.ontario.ca/page/inland-lakes-designated-lake-trout-management#section-1) and for other regions in Canada, using data in Minns et al. (28), and Alaska (https://www.adfg.alaska.gov/SF_Lakes/). The ice-on and ice-off dates for lakes located within or adjacent to Algonquin Provincial Park (Lake of Two Rivers, Smoke, Tea, and Canoe Lakes) were obtained from the Algonquin Park Ice Conditions monitoring program (https://www.algonquinpark.on.ca/images/iceout_graph.jpg). For lakes within the IISD-ELA, ice phenology records were obtained from annual monitoring data (69), as well as for Alexie Lake (21). For the remaining study sites, including Lake Simcoe and Lake Papineau, ice phenology were roughly derived from citizen observations, remote sensing data (https://worldview.earthdata.nasa.gov/), or ice phenology records by Sharma et al. (70).

ACKNOWLEDGMENTS. This work was supported by grants from the Natural Sciences and Engineering Research Council (NSERC) of Canada (ALLRP 556300-20; RGPIN-2022-03162). We acknowledge the support from the SCT project for supporting work on Algonquin lakes, Kenauk Nature, and NSERC for work on Lake Papineau, Fisheries and Oceans Canada and DeBeers Canada for work on Alexie Lake, and the Lake Simcoe Protection Plan for work on Lake Simcoe. Additional support was provided by NSERC (RGPIN-2021-06542; RGPIN-2016-04016; RGPIN-2022-03162), CFI (Project # 33581), the Canada Research Chairs program and the IISD ELA for supporting activities on lakes in that region.

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